

THE RATE OF OVIPOSITION IN THE FRUIT FLY, DROSOPHILA

HERBERT SHAPIRO

(From the Zoölogical Laboratory, Columbia University, and the Marine Biological Laboratory, Woods Hole, Mass.)

As a subject attracting interest because of economic applications, egg-laying has been studied in the house fly and in other insects with a view to determining the factors affecting the total number of ova deposited. Because of its possible bearing on a question which was formerly under investigation by the author, an examination of the rate of egg production in the fruit fly *Drosophila melanogaster* was undertaken for the determination of individual variations, and the similarities, if any, among different mutants. It is not intended in this account to go into the possible experimental modification of oviposition rate nor to add anything to a treatment of the external influences affecting oviposition in insects in general (Richardson, 1925) but rather to describe the process as found under what may be called "normal" conditions for the life of this genus. Not only because of easy cultivation in the laboratory, eliminating special vivaria as may be required for other insects, but also due to the variety of effective media available (Pearl, 1926; Bridges, 1932) and the small amount of space necessary, *Drosophila* is a form very suitable for the study of egg-laying. Of greater moment is the fact that *Drosophila* lays eggs regularly over a longer period and in larger numbers as compared with the activity of certain other forms in these respects; the Cecropia moth, for example, requires only three or four days to lay its quota of several hundred eggs (Rau, 1910). An interesting and compact account of the biology of the pomace fly and complete references up to 1925 are contained in the monograph of Morgan, Bridges, and Sturtevant (1925); for this reason only a few experiments bearing on this study need be cited.

Castle and associates (1906) demonstrated that close inbreeding did not diminish the fertility of *Drosophila*, provided fertile pairs were selected to continue the stock. For a detailed account of the morphology of the ovary and the internal phenomena of reproduction, reference may be made to the description of Nonidez (1920), and of Laurinat (1931), while the courtship and other external phenomena of reproduction have been observed by Sturtevant (1915, 1921). That factors for egg size exist in all four linkage groups has been brought

out by Warren (1924), who also gives a description of the external appearance of the egg. The cytological events accompanying and consequent upon fertilization have been pictured by Huettner (1924).

Before proceeding further, it might be said that the general result of this investigation is that although the life span, active egg-laying period, and total egg output varied greatly from individual to individual in the various crosses, there is found fundamentally the same method of elaborating eggs, which is followed also in the cases of certain invertebrates other than *Drosophila* for which data are available in the literature, and to which reference will again be made. That is, to put the matter another way, a general equation for the rate of laying may be applied to the data secured.

The search for a means of securing the eggs readily and arranged so that they might be counted offered no real difficulty. It was found that if an agar gel was plated out on a small cardboard spoon about three inches long (such as was used, for example, in the experiments of Patterson, 1929) the cardboard would absorb water, leaving crevices in the surface of the gel. It was particularly desirable to avoid this inasmuch as flies will tend to deposit their eggs in these crevices, thereby rendering difficult the procedure of counting. This defect in the technic was remedied by impregnating the spoons with paraffin of high melting point (68°–70° C.). The medium upon which the flies could live and lay their eggs was prepared by adding 5 per cent of molasses to a hot 1 per cent solution of agar in distilled water. About 175 cc. of this medium would suffice for 110 spoons, into which the medium was poured and allowed to gel, forming a plate which adhered to the spoon, but which might, if desired, be cleanly and easily separated from the spoon in which it was cast. After cooling, a drop of yeast suspension in distilled water was placed on the surface of the "plate," which was tilted to allow the suspension to spread uniformly over the surface. These spoons, made up thus each evening, were then placed in crystallizing dishes, carefully covered to prevent access of foreign flies, and used the following day. The flies were secured soon after hatching, and placed individually in a vial four inches long and an inch in diameter together with one of the spoons. The vial was then plugged with cotton. At approximately 24-hour intervals throughout the life of the fly, the spoon upon the surface of which the eggs were deposited was removed from the vial and a fresh spoon introduced. The eggs could then easily be counted under a binocular. Table I indicates how counts were recorded and includes also some derived data. Frequent examinations in the early stages of the work revealed no deposition of eggs on the walls of the vial or

TABLE I

A sample record. From the data (of an individual of cross k) presented in this table, the curves in Figs. 1 to 3 were drawn.

Date (1930)	Hour of removal of eggs	Number of eggs counted	Time elapsed	Total No. of eggs	Time in total
			<i>days</i>		
7/16	3:50 P.M.	11	1.00	11	0.4170
7/17	1:58 P.M.	70	1.92	81	0.4369
7/18	2:34 P.M.	102	2.95	183	0.5663
7/19	3:05 P.M.	125	3.98	308	0.6946
7/20	3:02 P.M.	116	4.98	424	0.8232
7/21	2:41 P.M.	148	5.97	572	0.9403
7/22	2:06 P.M.	102	6.96	674	1.069
7/23	2:15 P.M.	136	7.97	810	1.190
7/24	2:17 P.M.	115	8.97	925	1.313
7/25	2:47 P.M.	126	10.00	1051	1.437
7/26	3:06 P.M.	127	11.01	1178	1.557
7/27	3:03 P.M.	124	12.01	1302	1.675
7/28	12:28 P.M.	78	12.90	1380	1.784
7/29	2:51 P.M.	139	14.00	1519	1.911
7/30	2:57 P.M.	92	15.01	1611	2.032
7/31	10:18 A.M.	72	15.81	1683	2.129
8/1	12:03 P.M.	93	16.88	1776	2.256
8/2	10:42 A.M.	98	17.82	1874	2.365
8/3	12:08 P.M.	87	18.88	1961	2.491
8/4	11:38 A.M.	83	19.86	2044	2.606
8/5	11:27 A.M.	61	20.85	2105	2.725
8/6	11:09 A.M.	79	21.84	2184	2.840
8/7	11:25 A.M.	46	22.85	2230	2.964
8/8	11:30 A.M.	57	23.85	2287	3.083
8/9	10:08 A.M.	51	24.79	2339	3.196
8/10	11:11 A.M.	42	25.84	2380	3.324
8/11	12:10 P.M.	30	26.88	2410	3.452
8/12	11:43 A.M.	44	27.86	2454	3.569
8/13	10:46 A.M.	29	28.82	2483	3.687
8/14	11:07 A.M.	41	29.84	2524	3.809
8/15	11:09 A.M.	35	30.84	2559	3.930
8/16	9:41 A.M.	16	31.78	2575	4.047
8/17	11:07 A.M.	25	32.84	2600	4.176
8/18	10:43 A.M.	16	33.82	2616	4.298
8/19	10:50 A.M.	14	34.82	2630	4.421
8/20	10:40 A.M.	11	35.81	2641	4.545
8/21	11:27 A.M.	8	36.84	2649	4.675
8/22	11:04 A.M.	6	37.83	2655	4.798
8/23	11:08 A.M.	7	38.84	2662	4.925
8/24	10:01 A.M.	4	39.79	2666	5.044
8/25	10:43 A.M.	7	40.82	2673	5.173
8/26	10:47 A.M.	2	41.82	2675	5.299
8/27	10:58 A.M.	1	42.83	2676	5.427
8/28	10:20 A.M.	6	43.80	2682	5.548
8/29	11:29 A.M.	2	44.85	2684	5.681
8/30	10:00 A.M.	0	45.78	2684	5.799
8/31	10:28 A.M.	0	46.81	2684	5.929
9/1	11:07 A.M.	0	47.84	2684	6.059
9/2	11:46 A.M.	dead	48.88	2684	6.191

elsewhere on the spoon other than the surface of the gel, so that search for eggs in these locations was not thereafter regularly made. The eggs, being white, and 0.5 mm. in length, stand out clearly against the brown medium. Occasionally recounts were made, and it was found that quite consistently all the eggs would be included in a count. In handling the vials there was a minimum of shaking to avoid any possibility of disturbing the laying activities of the flies. The work was greatly facilitated by the use of an incubator in which the flies were kept at $24^{\circ}\text{C.} \pm 1^{\circ}\text{C.}$; and for preventing the vials from rolling about, and to maintain the surface of the medium level, by the availability of racks which had been designed by Doctor Calvin B. Bridges, and kindly loaned by him.

The results reported here comprise observations on the complete egg-laying history of some 93 females. Virgins, mated flies, and flies kept with more than one male were followed; while in the case of *Drosophila obscura*, which has been studied extensively by Lancefield (1929), both species or physiological races, Race *A* and Race *B*, were observed. Thus with *Drosophila melanogaster*, these crosses were made:

- a. Type (wild) females (virgins).
- b. $+ \sigma^{\text{♂}} \times + \text{♀}$ ($\sigma^{\text{♂}}$ removed after mating).
- c. $+ \sigma^{\text{♂}} \times + \text{♀}$ (with male).
- d. $+ \sigma^{\text{♂}} \times + \text{♀}$ (with 2 males. In all cases males were replaced if their death occurred before that of the female.)
- e. Vestigial females (virgins).
- f. $\text{vg } \sigma^{\text{♂}} \times \text{vg } \text{♀}$ (with male).
- g. $+ \sigma^{\text{♂}} \times \text{vg } \text{♀}$ (with male).
- h. $+ \text{♀} \times \text{vg } \sigma^{\text{♂}}$ (with male).
- i. Sepia $\sigma^{\text{♂}} \times \text{sepia } \text{♀}$ (with male).
- j. Siblings resulting from cross *h* were mated to each other (with male).
- k. Siblings resulting from cross *g* were mated to each other (with male).
- l. $\text{Lobe}^2 \sigma^{\text{♂}} \times \text{Lobe}^2 \text{♀}$ (with male).

With *D. obscura*:

- a. Race *A* $\sigma^{\text{♂}} \times \text{Race } A \text{ ♀}$ (with $\sigma^{\text{♂}}$).
- b. Race *B* $\sigma^{\text{♂}} \times \text{Race } B \text{ ♀}$ (with $\sigma^{\text{♂}}$).
- c. Race *A* $\sigma^{\text{♂}} \times \text{Race } B \text{ ♀}$ (with $\sigma^{\text{♂}}$).
- d. Race *B* $\sigma^{\text{♂}} \times \text{Race } A \text{ ♀}$ (with $\sigma^{\text{♂}}$).

A few details of passing interest may be dealt with briefly. After the death of most of the flies the abdomen was opened, the ovaries dissected out, and the number of remaining well-formed eggs counted.

No correlation between this variable and any of the other factors studied could be found. The females varied with respect to their actual egg-laying period, some ceasing to produce eggs several or more days before death, others still laying, though at a much diminished rate, even to the end of the life span. Virgins, as well as mated flies, lay eggs regularly, a fact noted previously both by Hyde (1921) and by Hanson and Ferris (1929). The former remarks, "The fecundity record is apparently not modified as a result of fertilization for the unfertilized female lays eggs regularly and in large numbers," possibly implying that mating has no effect on the rate of laying, a point which will be dealt with again. Complete sterility was found in three flies; two of these contained mature eggs in the abdomen after death. In the third, which had large brown concretions around the spermathecae, the ventral receptacle and spermathecae were packed with motionless sperm.

The hybrid females (crosses *j* and *k*) displayed their vigor not only in the increased egg production, which was of the order of two or three times that of the mother or of the females of the stock from which the male parent was selected, but also by their incessant activity in the vials in which they were kept. It was more difficult to replace spoons from these vials than from others, an active fly being unfortunately, quicker than the hand.

In *D. melanogaster* laying commenced in general one to two days after hatching, though this period is prolonged in the case of some of the virgins to seven or eight days. Race *B* of *D. obscura* usually precedes egg-laying by a characteristic period of three days of non-productivity, while Race *A* females wait two days before giving off the first egg.

Figure 1 represents the egg-laying of one of the hybrids of cross *k*—a total of 2,684 eggs in a life of about 49 days. The set of data given by this fly was used also in plotting Figs. 2 and 3. In the first figure, where the total number of eggs is plotted against time, a sigmoid curve results. A similar figure appears for all the other flies, and all the data might indeed be represented in this fashion as a family of curves. For this purpose, however, a more convenient means of plotting is utilized, as will be seen in the last figure. A phenomenon peculiar to *D. obscura* appears also in the curves plotted for them. Most of the females of this genus are in the habit of stopping egg-laying at irregular intervals for a period of one or two days, and very occasionally, longer. This, nevertheless, does not affect the characteristic shape of the curves. These curves, as well as those succeeding, are quite generally representative of the entire group of curves drawn.

One would like to know the appearance of the daily egg-laying curve. Inasmuch as it was not practicable to make measurements at exact 24-hour intervals, and also because a further and more serious objection offers itself in the tendency of flies to lay eggs in irregular spurts, as described by Adolph (1920), who says, "There is a distinct tendency for an individual fly to lay several eggs within a few minutes.

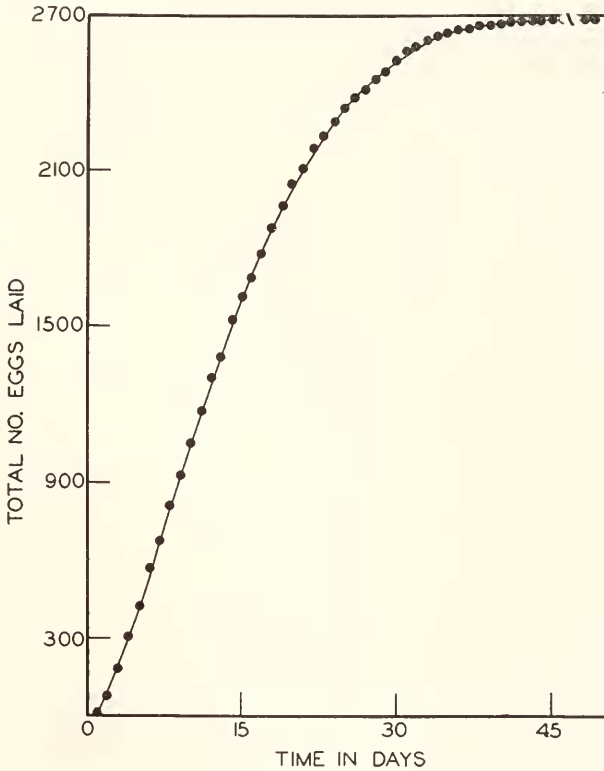


FIG. 1. The total number of eggs produced during the lifetime of a fly. These sigmoid integral curves are obtained also when the data from other individuals are similarly plotted. Figs. 1 to 3 inclusive are curves drawn from the records (contained in Table I) for the same female.

How often such spasms occur under uniformly stimulating conditions is unknown, but there is certainly no daily or weekly periodicity among different individuals," the data were not plotted simply as recorded. Guyénot (1913) remarks, ". . . la ponte se produit sous forme de décharges, causées par la surabondance des oeufs formés." The following means, consequently, were adopted for obtaining the curve shown in Fig. 2, a procedure which may be justified by a simple

hypothetical consideration, inadequate as it may be. The tendency to lay eggs in bunches has been noted. Thus, if at the height of its egg-laying period, a fly laid 120 eggs per day, it would not lay one egg regularly every twelve minutes as might be computed, but rather several eggs during this interval, and then none for perhaps the next half hour. For this reason one must have recourse to an integral curve, for considered from the standpoint of minutes, the egg-laying is irregular, but from the standpoint of days or weeks, it becomes quite regular.

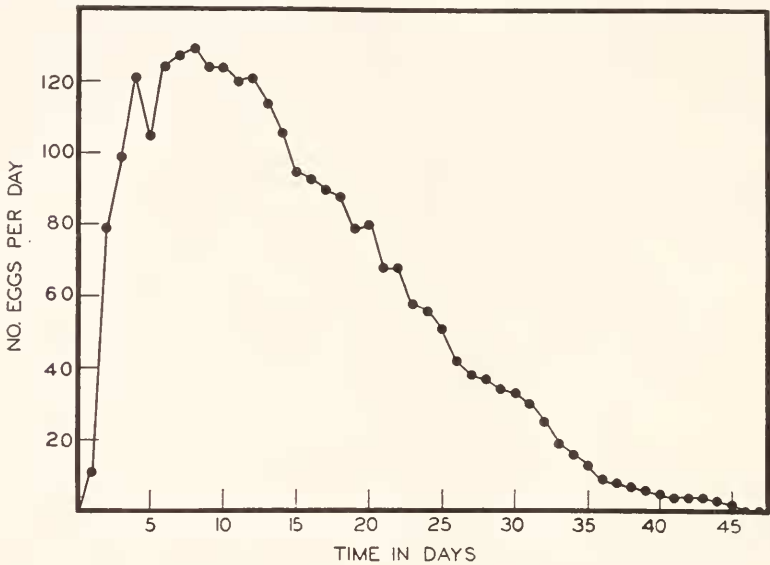


FIG. 2. The daily egg production. This curve was secured by graphical interpolation from an enlarged plot of Fig. 1.

A large integral curve similar to that shown in Fig. 1 was plotted on paper of dimensions $3\frac{1}{2} \times 4$ feet, and then, by use of the mirror tangentimeter described by Latshaw (1925), the number of eggs for each 24-hour interval could be pieced out of the curve with fair precision. The differential curve so secured rises to a maximum of about 130 eggs per day and then falls off gradually to zero at about the end of the fly's life. The area under the curve would represent the total number of eggs deposited. In the attempt to arrive at some general conclusions from the data, the figures were set up in a manner of which Table II is an example. No clean-cut generalizations suggested themselves from a study of such averages. With the apparent general similarity of the type of curve shown in Fig. 1 as drawn for

different individuals in mind, it was decided to study individual cases, to determine whether some general relationship might be found into which they all would fit.

It is found that if $t/\ln T$ is plotted against t , where t represents the time in days at which any given total (T) is attained, the points arrange themselves linearly, as may be seen by inspection of Fig. 3. It will be noted that the last four points are off the curve. This is due to the cessation, on the forty-fifth day, of egg-laying by the fly, which lived four days longer; the point for each of these post-laying days was calculated by using the same total, and these points arrange themselves along another line. The curve shown in Fig. 3 has been drawn also for each of the other 92 females studied and gives an equally good fit for these too, except three others where the points scatter rather more widely on each side of the line. All the sets of data might be

TABLE II
Cross $c : +\sigma^7 \times +\varphi$ (with male)

Total number of eggs laid	Life span	Day of cessation of egg-laying
	<i>days</i>	
755	27	27
617	20	18
1176	41	28
1537	41	40
830	36	33
1097	35	32
Average 1002 ± 109 (A.D.)	35 ± 2.5 (A.D.)	29.7 ± 1.2 (A.D.)

plotted in somewhat fan-shaped arrangement in the space of Fig. 3, those representing a smaller rate lying above the curve there drawn, those with a greater rate falling below. If instead of this the slope of each curve so obtained be plotted against the grand total of eggs produced, the points fall as found in Fig. 4.

From Fig. 3 it follows that

$$\frac{t}{\ln T} = at + b,$$

where t and T remain with the same meaning indicated previously, a and b representing respectively the slope of the curve and its intercept on the y axis. This yields an equation for the total number of eggs (T) already produced at any stated time (t):

$$T = e^{\frac{t}{at+b}}.$$

To get the change in total with time, the first derivative is taken

$$\frac{dT}{dt} = \frac{be^{\frac{t}{a+b}}}{(at+b)^2},$$

and to arrive at the time at which the rate of egg-laying is at its maximum, the second derivative is taken, set equal to zero, and solved

$$\frac{d^2T}{dt^2} = \frac{be^{\frac{t}{a+b}}[b - 2a(at+b)]}{(at+b)^4},$$

$$t = \frac{b}{2a^2}(1 - 2a)$$

For the fly whose data are plotted as shown in the figures, this maximum is thus calculated to be 5.7 days, when the values used for the constants a and b are 0.121 and 0.221, whereas the value found by inspection of Fig. 2 is about 7.5 days.

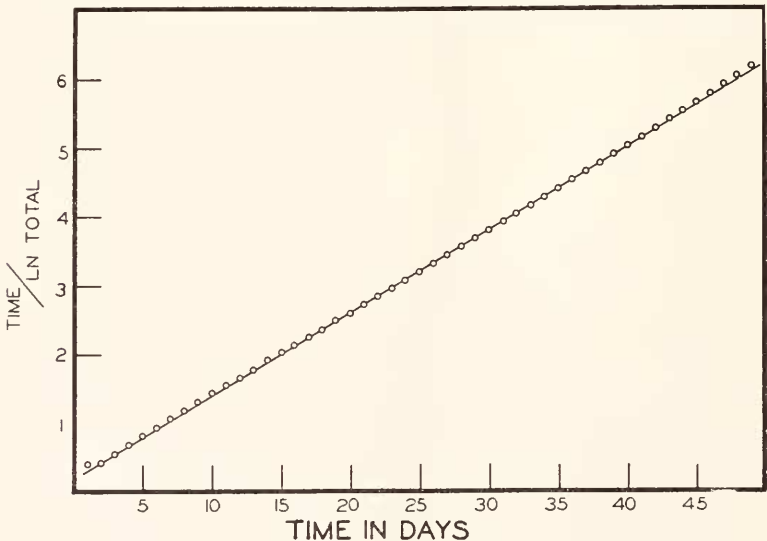


FIG. 3. A typical curve, demonstrating the linear relationship between the variables indicated.

The oviposition data are tabulated in the literature for the cases of some other invertebrates. These have been examined and found to fit the formulation just shown. They are as follows:

Hyde (1921) reported what were considered three unusual cases of fecundity for mated *D. melanogaster* females, namely, totals of 1,613, 1,807, and 2,184 eggs. Similar values have been found quite regularly

in the animals studied here, and with respect to the hybrids it is rather the rule for them to lay 2,000 to 3,400 eggs. Fauré-Fremiet and Garrault (1928) give data for the egg production of *Margaropus australis*, an acarid. While studying the growth of the snail *Lymnaea columella*, Baily (1931) recorded also the egg-laying. The empirical equation applies also to the data presented by these authors, though not quite so well for some of the individuals of the last-mentioned instance as for *Drosophila* due to the more pronouncedly intermittent character of egg production in the snails; however, there is a definite fit. A curve plotted for one of the sets of data presented by each of

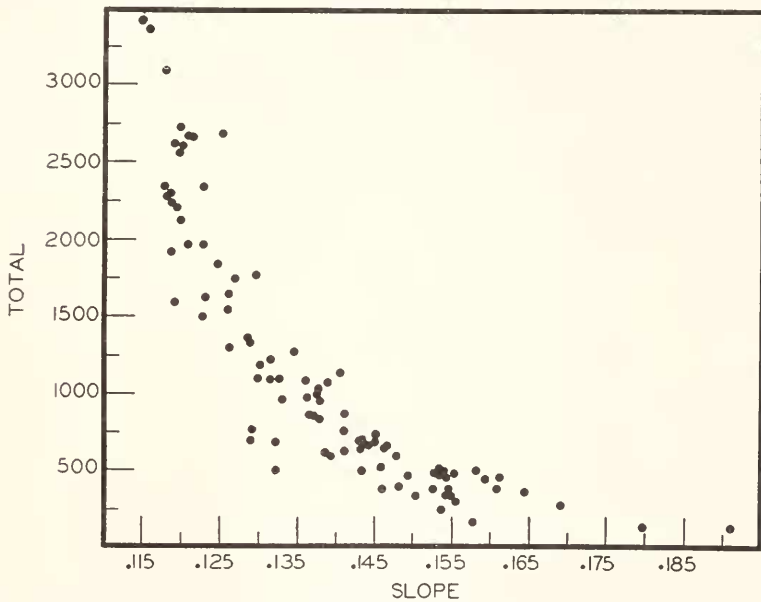


FIG. 4. Each point represents the slope (of a curve plotted as in Fig. 3) in relation to the sum total of eggs produced, for each of the flies studied.

these authors is presented in Fig. 5, where it may be compared, for example, with the curve for the data derived from a female of cross *a* (*D. obscura*).

It is to be pointed out here that it follows from what has been described that unless one is certain that females are producing eggs at the same rate, it is not a sound procedure to select flies at random from a stock and use some for experimentation dealing with egg production, and others for controls, and then to compare the averages of the results. This comparison might possibly lead to erroneous conclusions. From the nature of Fig. 2, it becomes evident that it

should be determined that the shapes of the egg-laying curves for both controls and experimental material, both as regards height of the maximum and length of the curve, are reasonably similar at the outset. In connection with this, an analogous situation may be cited. Davenport (1931) inveighs against the procedure of drawing conclusions concerning growth processes from accumulated data. From the mass statistics of 100,000 children, one might decide that the velocity of growth is greatest at two periods, one in intra-uterine life, and one at about 14.5 years (in the case of the male). When, however, the study

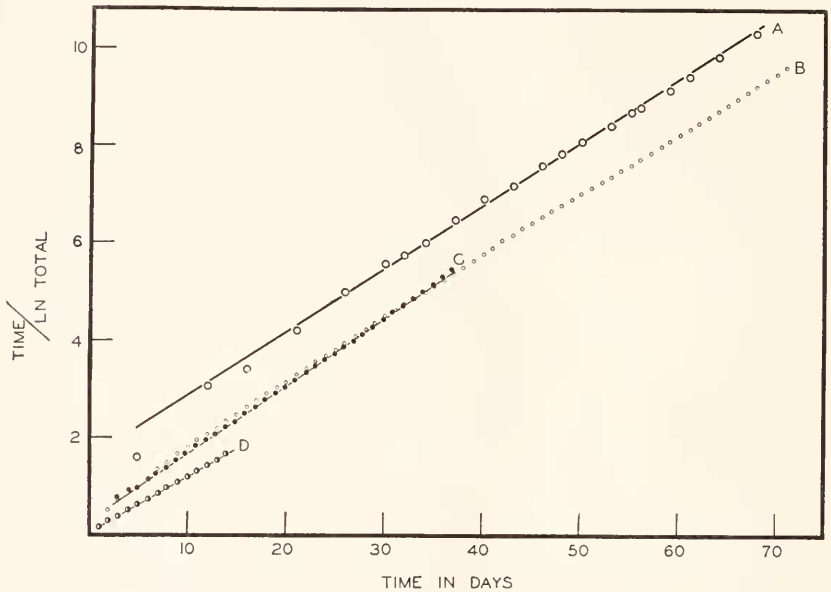


FIG. 5. Comparison of the curves of various invertebrates. *A*, of a snail *Lymnaea columella* (data of Baily); *B*, of *D. melanogaster* (data of Hyde); *C*, of *D. obscura* (Race A); *D*, of a tick, *Margaropus australis* (data of Fauré-Fremiet and Garrault). In *A* the egg output amounted to 725; in *D*, 4346 eggs were produced.

of individual children is made, the resulting curve of growth is found to be very different from that of the mass curves, and varies with different children. Instead of the maximum being reached rather gradually at the age of 14.5 years, a rapid growth of the individual at adolescence, of almost explosive rapidity, is found; the age at which this occurs, and its magnitude, varying with the individual.

When one is dealing with a constantly changing quantity, and where this rate of change will vary for different flies at the same age, the averaging of data will give only a very approximate idea of what

is occurring in general in individual cases. If the proper flies be used, one may see that by averaging different kinds of curves such as are presented in Fig. 2, provided their maxima and duration be different, any kind of average curve, within limits, may be produced. This may perhaps account for the differences observed by Hanson and Ferris (1929), when in one experiment the averaged laying curve for mated white flies rose to a maximum of about 24 eggs per day, while in another similar experiment a maximum of about 52 eggs per day was reached. The maxima of averaged curves may be shifted depending on the nature of the maxima of the individual curves being averaged.

Hanson and Ferris decide from their own data presented as averages that mating results in heightened productivity by the female. There is lack of agreement as to whether or not, in general, the male serves to stimulate an increased production of eggs. Guyénot (1913) states that there is a considerable delay, which varies from case to case, in the initiation of egg-laying by certain *Drosophila* virgins, but that, once commenced, their production gradually approaches in intensity that of the mated individual. In the cases observed by the writer, the vestigial virgins started to lay eggs the second day after hatching, and produced eggs regularly thereafter, whereas type virgins delayed laying from two to eight days after hatching. It is of interest to note that examination of the data shows that certain of the virgins produced more eggs during their life than did mated flies, and this in females from a stock which had been well inbred; although the averages were greater for mated flies than for virgins. These figures, with the deviation of the mean (A.D.), are listed here; the numbers in parentheses represent the number of individuals whose data are averaged.

+ virgins	677 ± 116	(8).
+ ♂ × + ♀ (without male)	718 ± 103	(12).
+ ♂ × + ♀ (with male)	1091 ± 115	(7).
+ ♂ × + ♀ (with two males)	1402 ± 98	(4).

Inasmuch as certain virgins, for example, will lay many more eggs than certain mated flies, one would hesitate to reach the generalization from these averages alone that mating stimulates the female to increased egg production, and cannot help suspecting that the increase may not be an intrinsic one. Eight type virgins laid the following numbers of eggs in the time in days indicated in parentheses: 165 (47), 378 (28), 400 (55), 454 (70), 698 (40), 758 (42), 1088 (70), 1474 (31). In view of the great individual variations, the averaging of the records of much greater numbers of individuals would be required to give a definite statistical answer. It might seem that a means may be

afforded for obtaining an indication of the course of events, in *Drosophila* at least, by use of the equation described above. If mating results in increasing constantly and continuously the rate of egg production, then plotting as in Fig. 3 the data of an experiment where a virgin lays eggs for a given period and is then mated, there should be a break in the line toward the abscissa after the time of mating. Due, however, to the logarithmic nature of the plot, small deviations or changes in the rate do not become readily manifest; consequently this bend is not accentuated sufficiently to permit a definite and unequivocal separation of the parts of the curve that would result.

In an investigation of egg-laying in the domestic fowl, Fauré-Fremiet and Kaufman (1928) advance the interesting hypothesis supported by histological evidence of what is termed a constant probability of transformation of oöcytes, an interpretation entirely independent of the idea of senescence as offered by Brody, Henderson, and Kempster (1923). In seeking a factual basis for this idea, the first-mentioned authors studied the formation of oöcytes in the hen, and the initial number of oöcytes, and proposed an interpretation of the curve of laying according to such data. After a review of the experimental work done on this phase of the subject, it appears that the activity of the germinal epithelium can be restored in certain pathological or experimental conditions (Pearl, 1921), but they conclude that in the hen, under normal conditions, the number of oöcytes is quite limited after birth. Subsequent to birth, oöcytes of the chick grow slowly and progressively. During the period of egg-laying (which may be of eight years' duration) some of the oöcytes undergo a very rapid growth and increase their vitelline mass a hundred-fold in five to eight days, following which they may be laid.

They propose then the following equation, similar to that of Brody and collaborators, to describe the decrease in rate of egg-laying:

$$N_t = N_0 e^{-Kt},$$

where N_t = the number of oöcytes still available at time t (reckoned in years), N_0 = the initial number of available oöcytes, e = the base of natural logarithms, and K = a constant. The average curve of decrease in a given race in an individual is said then to depend on two values: N_0 , the initial number, representing the stock of available oöcytes; the other they term the probability of transformation of oöcytes, a meaning which is attached to the value K , and $1/K$ or θ , would represent the average life of the oöcyte, or the average period during which the oöcytes can remain at the initial state before undergoing the very rapid growth of yolk accumulation. These constants

are supposedly independent of environment, and are probably, according to the authors, hereditary. It is apparent that this equation is formally tantamount to that for a first order reaction, *viz.*,

$$K = \frac{1}{t} \ln \frac{a}{a - x},$$

where the rate of change of the concentration of substance *A* at any instant is proportional to its concentration at that instant; *t* represents time, *a* the original molar concentration, and (*a* - *x*) the concentration of *A* after *t* minutes. When stated in terms of egg-laying this would mean simply, aside from any implications of a chemically analogous factual basis, that at any instant the rate of decrease of the number of eggs laid is proportional to the number of eggs remaining unlaidd.

This equation proposed by Brody, Henderson and Kempster, or the equivalent one of Fauré-Fremiet and Kaufman, for averaged data of egg production by the hen, cannot be carried over to the situation presenting itself in *Drosophila*, where the rise in egg-laying to a maximum is a regular, intrinsic part of the process. The equation of Fauré-Fremiet and Kaufman can be applied only to the descending portion of the curve of laying of the tick *Margaropus australis*, whereas the equation for *Drosophila* can apply also to the entire curve for *Margaropus*. In the case of the arthropod, then, the hypothesis of a probability of transformation of oöcytes appears to be inadequate. To bridge the discrepancy between the curve for laying of *Margaropus* and of the hen, Fauré-Fremiet and Garrault (1928) introduce the conception of the progressive development of a "physiological factor," that is to say, of a complex of somatic conditions allowing yolk accumulation, as being probably responsible for the ascending portion of the curve. Inasmuch as a general equation is found which applies to the whole process, it is perhaps more desirable to conceive it as continuous, and operating throughout as part of the same mechanism, rather than to introduce the idea of a dichotomy, the operation of the second process remaining in abeyance until the completion of the first. However, the existence of such a factor as the first, not yet yielding to exact treatment, is by no means excluded.

Grateful acknowledgment is due Professor D. E. Lancefield and Professor A. H. Sturtevant for reading and criticizing the manuscript.

SUMMARY

The rates of egg-laying of certain mutants of *Drosophila melanogaster* and of two races of *Drosophila obscura* were studied and compared with certain other cases for which data are presented by the authors.

The fecundity of hybrids of *Drosophila melanogaster* was also studied. An empirical equation describes the egg-laying curves of all the flies studied (about 93 in number) and is $T = \frac{t}{e^{at+b}}$ where T represents the total number of eggs already laid at the time t , and e is the base of natural logarithms. The constants a are shown to be correlated with the total number of eggs deposited.

LITERATURE CITED

- ADOLPH, E. F., 1920. Egg-laying Reactions in the Pomace Fly, *Drosophila*. *Jour. Exper. Zool.*, **31**: 327.
- BAILY, J. L., 1931. Some Data on Growth, Longevity, and Fecundity in *Lymnæa columella* Say. *Biologia Generalis*, **7**: 407.
- BRIDGES, C. B., 1932. Apparatus and Methods for *Drosophila* Culture. *Am. Nat.*, **66**: 250.
- BRODY, S., E. W. HENDERSON, AND H. L. KEMPSTER, 1923. The Rate of Senescence of the Domestic Fowl as Measured by the Decline in Egg Production with Age. *Jour. Gen. Physiol.*, **6**: 41.
- CASTLE, W. E., F. W. CARPENTER, A. H. CLARK, S. O. MAST, AND W. M. BARROWS, 1906. The Effects of Inbreeding, Cross-breeding, and Selection upon the Fertility and Variability of *Drosophila*. *Proc. Am. Acad. Arts and Sci.*, **41**: 731.
- DAVENPORT, C. B., 1931. Individual vs. Mass Studies in Child Growth. *Proc. Am. Philos. Soc.*, **70**: 381.
- FAURÉ-FREMIET, E. ET H. GARRAULT, 1928. La courbe de décroissance de ponte chez *Margaropus australis*. *Ann. de Physiol.*, **4**: 218.
- FAURÉ-FREMIET, E., ET L. KAUFMAN, 1928. La loi de décroissance progressive du taux de la ponte chez la Poule. *Ann. de Physiol.*, **4**: 64.
- GUYÉNOT, ÉMILE, 1913. Études biologiques sur une mouche, *Drosophila ampelophila* Löw. VII. Le déterminisme de la ponte. *Compt. Rend. Soc. Biol. Paris*, **74**: 443.
- HANSON, F. B., AND F. R. FERRIS, 1929. A Quantitative Study of Fecundity in *Drosophila melanogaster*. *Jour. Exper. Zool.*, **54**: 485.
- HUETTNER, A. F., 1924. Maturation and Fertilization in *Drosophila melanogaster*. *Jour. Morph.*, **39**: 249.
- HYDE, R. R., 1921. A High Fecundity Record for *Drosophila melanogaster*. *Proc. Ind. Acad. Sci.*, **31**: 259.
- LANCEFIELD, D. E., 1929. A Genetic Study of Crosses of Two Races or Physiological Species of *Drosophila obscura*. *Zeitschr. f. ind. Abstammungs- u. Vererbungslehre*, **52**: 287.
- LATSHAW, M., 1925. A Simple Tangentimeter. *Jour. Am. Chem. Soc.*, **47**: 793.
- LAURINAT, K., 1931. Über den Einfluss des Keinzellalters auf das Geschlechtsverhältnis bei *Drosophila melanogaster*. *Zeitschr. f. ind. Abstammungs- u. Vererbungslehre*, **57**: 139.
- MORGAN, T. H., C. B. BRIDGES, AND A. H. STURTEVANT, 1925. The Genetics of *Drosophila*. *Bibliographia Genetica*, **2**: 1.
- NONIDEZ, J. F., 1920. The Internal Phenomena of Reproduction in *Drosophila*. *Biol. Bull.*, **39**: 207.
- PATERSON, J. T., 1929. The Production of Mutations in Somatic Cells of *Drosophila melanogaster* by Means of X-rays. *Jour. Exper. Zool.*, **53**: 327.
- PEARL, R. AND W. F. SCHOPPE, 1921. Studies on the Physiology of Reproduction in the Domestic Fowl. XVIII. Further Observations on the Anatomical Basis of Fecundity. *Jour. Exper. Zool.*, **34**: 101.

- PEARL, R., 1926. A Synthetic Food Medium for the Cultivation of *Drosophila*. *Jour. Gen. Physiol.*, 9: 513.
- RAU, P., 1910. Observations on the Duration of Life, on Copulation and on Oviposition in *Samia cecropia* Linn. *Trans. Acad. Sci. St. Louis*, 19: 21.
- RICHARDSON, C. H., 1925. The Oviposition Response of Insects. U. S. Dept. of Agriculture. Department Bulletin No. 1324. 17 pp.
- STURTEVANT, A. H., 1915. Experiments on Sex Recognition and the Problem of Sexual Selection in *Drosophila*. *Jour. An. Behav.*, 5: 351.
- STURTEVANT, A. H., 1921. The North American Species of *Drosophila*. *Carnegie Inst. Wash.*, publ. 301. 150 pp., 3 pl.
- WARREN, D. C., 1924. Inheritance of Egg Size in *Drosophila melanogaster*. *Genetics*, 9: 41.